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LEAF AND CORM  
TUNIC STRUCTURE IN  
*LAPEIROUSIA*  
(IRIDACEAE–IXIOIDEAE)  
IN RELATION TO  
PHYLOGENY AND  
INFRAGENERIC  
CLASSIFICATION<sup>1</sup>

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ABSTRACT

The tropical and southern African *Lapeirousia*, comprising 35 species, divides into two subgenera on the basis of leaf type. Leaf anatomy of eight species of *Lapeirousia* and selected species of the other five genera of Watsonieae was examined and compared with that of the putatively primitive *Pillansia*. *Lapeirousia* subg. *Lapeirousia* has corrugate leaves that lack a distinct midvein and are anatomically specialized in having predominantly or exclusively alternate vascular bundles and square, truncate costal ridges in which the epidermal cells are abruptly enlarged and often heavily thickened in the outer periclinal walls. This derived leaf structure correlates with the specialized woody corm tunics of the subgenus. Subgenus *Paniculata* has plane leaves with a distinct midvein, vascular bundles usually opposite, and rounded costal ridges with epidermal cells gradually diminishing in size and usually without a heavily thickened outer periclinal wall, the basic type for the tribe. Species of subg. *Paniculata* also have hard corm tunics composed of densely compacted fibers, the basic type for the clade including *Lapeirousia*. Several morphological characters within both subgenera of *Lapeirousia* were used in the construction of a cladogram indicating the major lineages in the genus. This forms the basis for our infrageneric classification that recognizes two subgenera, each with two sections.

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The 35 species of *Lapeirousia* (Iridaceae–Ixioideae) occur primarily in the winter rainfall zone of southern Africa and in semiarid southwest tropical Africa, but a few species are widespread across sub-Saharan Africa. Based on its forked style branches and the absence of flavone *O*-glycosides, *Lapeirousia* was assigned to Watsonieae, one of three tribes of Ixioideae (Goldblatt, 1989, 1990a); Watsonieae also include *Watsonia* (52 species), *Thereianthus* (6 species), *Micranthus* (3 species), and *Savannosiphon* (1 species). All except the last are restricted to southern Africa. Until now relationships among the species of *Lapeirousia* have been obscure, and there has been no phylogenetic analysis of the genus nor any modern attempt to provide an infrageneric classification. Baker's (1892, 1896) recognition of three subgenera no longer has any utility, since his subg. *Anomatheca* is now regarded as a genus of tribe Ixieae. His

subgenus *Sophronia* included at most four species and merits at best sectional rank. In this paper we investigate the major differences among the species of *Lapeirousia*, namely the nature of the corm tunics and leaf structure, and use these features to establish a new infrageneric classification. This study has been made in conjunction with a systematic revision of *Lapeirousia* in tropical Africa (Goldblatt, 1990b).

Leaf structure and corm tunic structure vary in an apparently consistent pattern across species in tropical and southern Africa. That these two independent features are correlated suggests a major division in the genus into two groups, for which we propose subgeneric rank. The anatomical basis for the leaf variation is explored here, and we propose a phylogeny for the major species groups in *Lapeirousia* based on several independently varying characters (Table 2). We recognize subg. *Pani-*

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TABLE 1. Leaf anatomical characters for the species studied and voucher data. (*G & M* = *Goldblatt & Manning*.) All vouchers are housed at MO. Coding for each character is as follows with the primitive condition indicated by 0 and the derived states by 1, 2, or 3.

1. Blade profile transverse section: 0 plane, 1 zigzag, 2 elliptic, 3 elliptic and hollow
2. Pseudomidrib: 0 absent, 1 present
3. Rib profile: 0 rounded, 1 truncate
4. Vascular bundles: 0 opposite, 1 alternate
5. Marginal bundle: 0 absent, 1 present
6. Sclerenchyma bundle sheath: 0 phloem cap, 1 complete
7. Subepidermal marginal sclerenchyma: 0 absent, 1 present
8. Bundle position: 0 all subepidermal, 1 major bundles subepidermal and minor ones embedded
9. Leaf margins: 0 rounded, 1 flanged

Taxon	Number of character state									Voucher data
	1	2	3	4	5	6	7	8	9	
<i>Pillansia</i>										
<i>templemannii</i> L. Bolus	2	0	0	0	0	0	0	0	0	<i>Powrie s.n.</i>
<i>Watsonia</i>										
<i>aletroides</i> (Burm. f.) Ker	0	1	0	0	1	0	1	1	0	<i>Sidey 1754</i>
<i>laccata</i> (Jacq.) Ker	0	1	0	0	0	0	1	1	0	<i>Rycroft 2531</i>
<i>Micranthus</i>										
<i>alopecuroides</i> (L.) Rothm.	3	0	0	0	1	1	0	1	0	<i>Grant 3489</i>
<i>Thereianthus</i>										
<i>minutus</i> (Klatt) G. Lewis	0	1	0	0	1	1	0	1	1	<i>Bolus s.n.</i>
<i>spicatus</i> (L.) G. Lewis	0	1	0	0	1	1	0	1	1	<i>Grant 5027</i>
<i>Lapeirousia</i> subg. <i>Paniculata</i>										
Section <i>Paniculata</i>										
<i>avasmontana</i> Dinter	1	1	0	1	1	0	0	1	0	<i>G &amp; M 8798</i>
<i>bainesii</i> Baker	0	1	0	0	1	0	0	1	0	<i>G &amp; M 8808</i>
<i>coerulea</i> Schinz	1	1	0	1	1	0	0	1	0	<i>G &amp; M 8811A</i>
<i>gracilis</i> Vaupel	0	1	0	0	1	0	0	1	0	<i>Seydel 3419</i>
<i>otaviensis</i> R. Foster	0	1	0	0	1	0	0	1	0	<i>G &amp; M 8837</i>
<i>schimperi</i> (Aschers & Klatt) Milne-Redh.	0	1	0	0	1	0	0	1	0	<i>Grant 4507</i>
Section <i>Fastigiata</i>										
<i>corymbosa</i> (L.) Ker	0	1	0	0	1	1	0	1	0	<i>Gillett 4503</i>
<i>Lapeirousia</i> subg. <i>Lapeirousia</i>										
Section <i>Sophronia</i>										
<i>anceps</i> (L.f.) Ker	1	0	1	1	1	0	0	1	0	<i>Drège 8507a</i>
<i>odoratissima</i> Baker	1	0	1	1	1	0	0	1	0	<i>G &amp; M 8803</i>
<i>pyramidalis</i> (Lam.) Goldbl.	1	0	1	1	1	0	0	1	0	<i>Mauve &amp; Oliver 233</i>
Section <i>Lapeirousia</i>										
<i>divaricata</i> Baker	0	1	1	1	1	0	0	1	0	<i>Goldblatt 2754</i>
<i>Savannosiphon</i>										
<i>euryphylla</i> (Harms) Goldbl. & Marais	0	0	0	0	1	0	0	0	0	<i>Pawek 10753</i>

*culata* for species with plane leaves having a distinct central vein and with corm tunics composed of densely compacted fibers; subg. *Lapeirousia*, by contrast, is made up of species with corrugate (shallowly plicate) leaves lacking a distinct central vein and having corm tunics of uniformly woody texture.

Inflorescence structure and bract morphology appear to coincide with this division to some extent but the patterns of variation in these two features are complex and sometimes contradictory, indicating a degree of convergence that obscures the major patterns of variation. Our conclusions are presented in the form of a cladogram for which

TABLE 2. Characters used in the cladogram (Fig. 3). The derived (apomorphic) states are listed first followed by the presumed ancestral (plesiomorphic) conditions. Apomorphies for *Savannosiphon* are taken from Goldblatt (1989). Other possible synapomorphies for sect. *Fastigiata* are discussed in the text. Anatomical specializations for *L. corymbosa*, the only species of sect. *Fastigiata* known anatomically, are not included in the cladogram.

1. Corm bases flat—corm bases rounded
2. Corm tunics woody—corms tunics of compacted fibers
3. Margins of corm toothed/spiny—margins of corm not elaborated
4. Leaves corrugate—leaves plane and with a pseudomidrib
5. Major veins alternate—major veins opposite
6. Ribs truncate—ribs rounded
7. Stems angular—stems terete
8. Inflorescence a pseudopanicule—inflorescence a spike
9. Flower zygomorphic—flower actinomorphic
10. Bracts small—bracts relatively large
11. Bracts ± membranous and dry above at anthesis—bracts herbaceous
12. Capsules coriaceous—capsules woody
13. Plants short and inflorescence congested—plants tall and inflorescences not notably congested

the characters are either discussed here or are taken from completed work (Goldblatt, 1989, 1990b, c).

MATERIALS AND METHODS

Leaf sections were prepared by following a standard graded ethanol dehydration and wax embedding technique. Serial sections were mounted on slides and stained in saffranin, sometimes counterstained in fast green, and permanently mounted in Canada balsam. Leaves studied, with a few excep-

tions, were collected from living plants in the field and fixed in FAA. Leaves taken from herbarium specimens were rehydrated in aerosol OT. One leaf was examined for each of the species studied. Voucher information is cited in Table 1.

The cladogram (Fig. 3), based on the data matrix (Table 3), was constructed without the use of a computer.

CHARACTER ANALYSIS

CORM TUNICS

There are substantive differences between the corm tunics of the two subgenera of *Lapeirousia*. Members of subg. *Lapeirousia* have corms with tunics composed of concentric hard, woody layers with smooth surfaces. With age these layers generally fragment irregularly into smaller pieces but rarely become fibrous or cancellate (Fig. 1A, B). In contrast, the tunics of subg. *Paniculata* are composed of densely compacted layers, which sometimes have a nearly woody texture and decay in a different manner. They fray at the lower edges, breaking into regular vertical strips that become increasingly fibrous with age, and sometimes become distinctly netted above or entirely (Fig. 1C–E). The anatomical basis for the differences is unknown. Within the two subgenera there are differences of lesser significance. In several species of subg. *Lapeirousia* the lower margins of the tunics are ornamented with small teeth, whereas in other species the edges are simply rounded (Goldblatt, 1972). In subg. *Paniculata* the way in which the tunics age is often characteristic of species. Some have tunics that form more or less regular vertical strips at least at the base, but that do not become fibrous, whereas the development of a fibrous texture characterizes others. Based on comparison with the genera closely allied to *Lapeirou-*

TABLE 3. Data matrix for *Savannosiphon* and the major generic clusters of *Lapeirousia*, numbered as in Table 3. Presence of the specialized condition is denoted by x; absence by –.

Genus	Character number												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Savannosiphon</i>	–	–	–	–	–	–	x	–	x	–	–	x	–
<i>Lapeirousia</i>													
Subgenus <i>Lapeirousia</i>													
Section <i>Lapeirousia</i>	x	x	x	x	x	–	x	–	x	–	–	x	–
Section <i>Sophronia</i>	x	x	–	x	x	x	x	–	x	–	–	x	–
Subgenus <i>Paniculata</i>													
Section <i>Paniculata</i>	x	–	–	–	–	x	x	x	–	x	x	x	–
Section <i>Fastigiata</i>	x	–	–	–	–	x	x	x	–	x	–	x	x

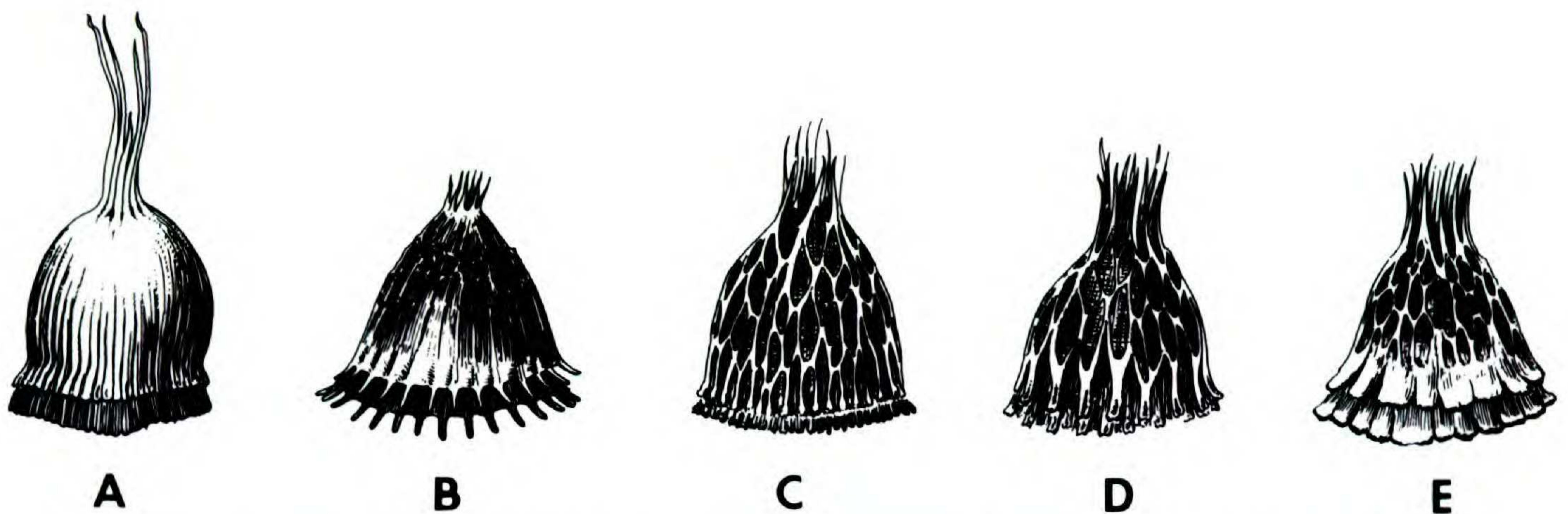


FIGURE 1. Representative corm tunics in *Lapeirousia*. Subgenus *Lapeirousia*:—A. *L. plicata* (Jacq.) Diels (Goldblatt 6052).—B. *L. dolomitica* Dinter (Nordenstam & Lundgren 1715). Subgenus *Paniculata*:—C. *L. bainesii* (Goldblatt & Manning 8808).—D. *L. coerulea* (Seydel 2609).—E. *L. micrantha* (Klatt) Baker (Williams 875). (Variously magnified.)

*sia*, we conclude that tunics composed of compacted fibers are the primitive condition. Similar, though not identical, tunics occur in *Thereianthus* and *Micranthus*, corms of which can often only be distinguished from those of *Lapeirousia* by being rounded (vs. flat) at the base. Woody tunics are unknown in other genera of Watsonieae, but are present in a few genera of Ixieae (notably *Hesperantha*, *Geissorhiza*, and *Romulea*) where they are most likely also a derived condition.

#### LEAF ANATOMY (Table 1)

Like all Iridaceae, the leaves of *Lapeirousia* are ensiform and equitant, and consist of a sheathing base and a blade that is typically lanceolate to linear and either plane or occasionally terete (subg. *Paniculata*), or ridged to corrugate (subg. *Lapeirousia*). In transverse section the blades are isobilateral and monofacial, oblong to linear, and variously plane-sided, ridged or zigzag. The marginal subepidermal cells are un lignified apart from the phloem cap that is present in most species, the basic condition for Watsonieae and presumably for the whole family. The intercostal epidermal cells are brick-shaped and thin-walled, although the outer periclinal walls may sometimes be slightly thickened. There is a notable correlation between leaf anatomy and subgeneric limits in the structure of the costal epidermis (Table 1). In subg. *Lapeirousia* the costal cells are abruptly enlarged and often heavily thickened in the outer periclinal walls, and the ridge is square and truncate (Fig. 2B). In subg. *Paniculata* the epidermis cells gradually diminish in size and usually lack a heavily thickened outer periclinal wall, and the ridges are smoothly rounded (Fig. 2A).

The vascular bundles are in two rows with larger

(major) bundles separated by one or two smaller (minor) bundles; major bundles occupy the ridges and minor ones the intervening troughs. The xylem poles face the center of the leaf. The two subgenera differ somewhat in the arrangement of the bundles. Although the major bundles are, with one exception (Table 1), alternate in subg. *Lapeirousia* (Fig. 2B), they are mostly, but not always, opposite in subg. *Paniculata* (Fig. 2A). This is an obvious determinant of the zigzag leaves in subg. *Lapeirousia* and plane leaves in subg. *Paniculata*. (In species with largely alternate bundles the central bundles are often opposite, but the pairs become more alternate distally.) The zigzag leaf form is a specialization in subg. *Lapeirousia*, and the accompanying alternation of the major bundles is probably so, given that all other genera of Watsonieae have opposed bundles. A pseudomidrib formed by larger central bundles is not evident in subg. *Lapeirousia* even though the central bundle in *L. divaricata* is sufficiently large to form a pseudomidrib. This species resembles subg. *Paniculata* in having opposite bundles, but the ridges are those of subg. *Lapeirousia*, and the corm tunics place it firmly in the latter. The opposed bundles in *L. divaricata*, a fairly specialized species, are presumably secondary. A pseudomidrib is present in all plane-leaved species of subg. *Paniculata*, even those in which the vascular bundles are alternate (*L. coerulea* and *L. avasmontana*), as well as in nearly all species of the tribe, and this is undoubtedly the basic condition. The alternation of bundles in *L. coerulea* and *L. avasmontana*, thought to be the most primitive species in subg. *Paniculata*, is puzzling. On the basis of outgroup comparison, this must be viewed as a specialization for the two species.

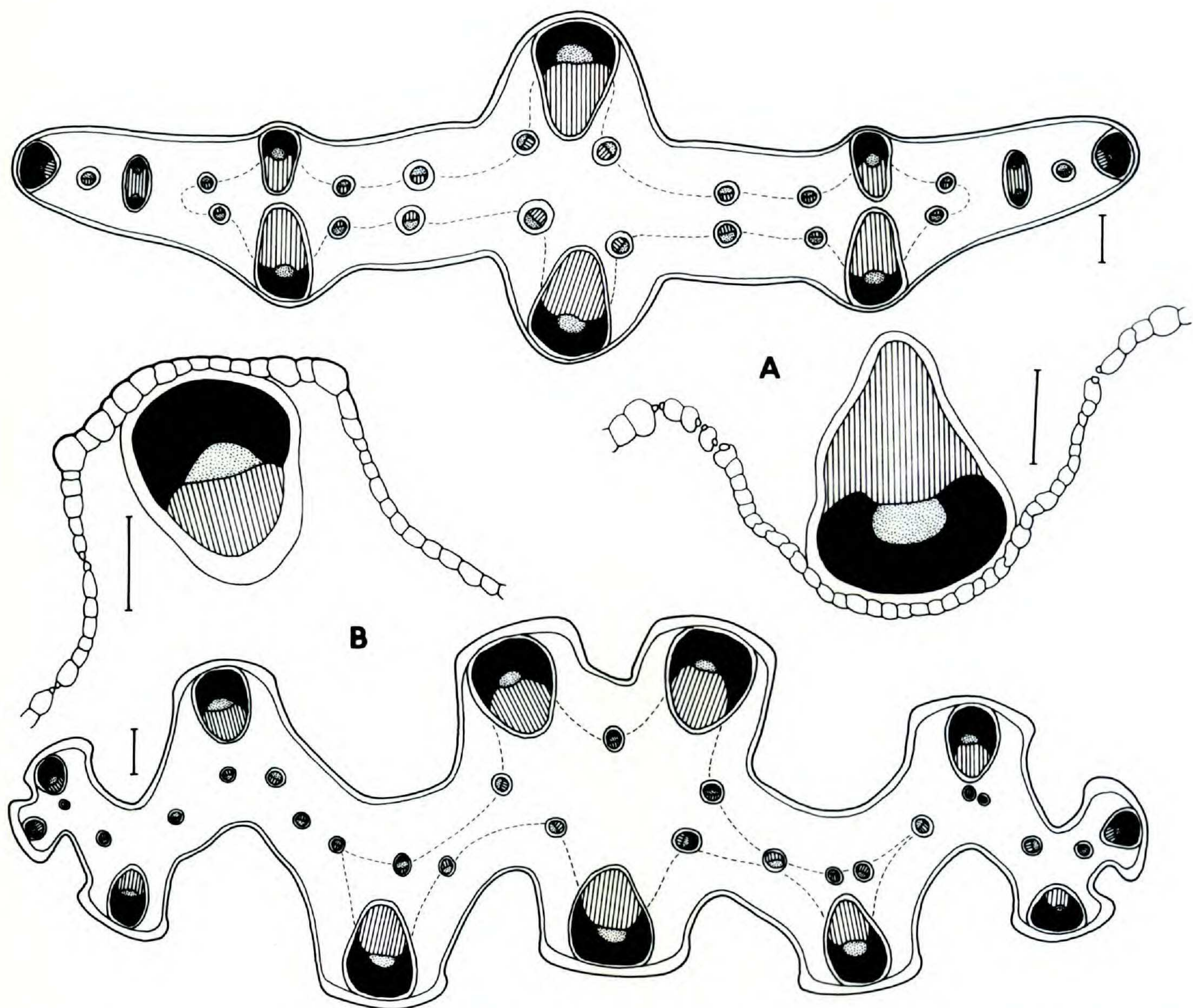


FIGURE 2. Transverse sections of leaf blades and vascular bundles in *Lapeirousia*. —A. Subgenus *Paniculata*: *L. bainesii*. —B. Subgenus *Lapeirousia*: *L. odoratissima*. Scale bars = 150  $\mu\text{m}$ . (Voucher data in Table 2.)

The major bundles reach the epidermis or are separated from it by a single layer of parenchyma, while the minor bundles are a number of cell layers below the epidermis. In species with opposite bundles, some vascular bundles may fuse at the xylem poles. An outer bundle sheath is present as a single layer of parenchymatous cells distinct from the surrounding mesophyll cells. An inner sheath is present as a phloem cap in at least the central major bundles, and usually all major bundles; and the phloem cap may also occur in some minor bundles. (In *L. corymbosa* alone there is a more or less complete sclerenchyma sheath, which is more tenuous at the xylem pole and is restricted to the central bundles.) Even when the phloem cap is absent from some minor bundles, the marginal bundles are still usually capped (but not in *L. anceps*, *L. pyramidalis*, and *L. corymbosa*). Crystals are present, mainly in the outer bundle sheaths but also in isolated mesophyll cells. Chlorenchyma may

be distinct from the central ground tissue or may grade into it.

*Pillansia*, the only genus of Ixioidae–Pillansieae, and the other genera of Watsonieae (*Savannosiphon*, *Micranthus*, *Thereianthus*, and *Watsonia*) each differ from *Lapeirousia* in some aspect of their leaf anatomy (Table 1). *Pillansia* is characterized largely by primitive traits (Goldblatt, 1990a). The leaf is plane in transverse section, and lacks a distinct midrib and ridges, although it is thickened toward the center and the profile is undulate. The epidermal cells are uniformly square without differentiation between costal and intercostal, although stomata are restricted to the intercostae. The vascular bundles are in two opposite rows of alternating major and minor pairs, and all except one or two very minor bundles are subepidermal and reach the epidermis, although the outer sheath is not distinct from the surrounding chlorenchyma at the phloem pole. All bundles have

a sclerenchyma phloem cap. A marginal bundle is absent, and there is no subepidermal marginal sclerenchyma.

In *Savannosiphon* the plane leaf also has all the vascular bundles subepidermal and of similar size. In *Micranthus* most of the bundles are subepidermal with some of the very minor bundles more deeply embedded in the leaf. All major bundles, including the marginal ones, have a complete sclerenchyma sheath well-developed at both poles. *Thereianthus* is likewise characterized by a complete sclerenchyma sheath around the major bundles, at least those in the center of the leaf, but the minor bundles have a phloem cap only and are embedded in the mesophyll. The marginal bundles lack sclerenchyma. We assume that a complete sclerenchyma sheath is a synapomorphy for *Micranthus* and *Thereianthus*. The latter differs further from the other genera in having nonvascularized flanges on the leaf margins, but not all species of the genus have been examined for this character. *Watsonia* resembles most species of *Lapeirousia* subg. *Paniculata* in the distribution and nature of the vascular bundles: two opposed rows of large subepidermal bundles separated by embedded minor bundles with sclerenchyma largely restricted to the phloem cap. It is distinct in the tribe in the extensive development of subepidermal sclerenchyma in a V- or U-shaped region at the leaf margin, associated with and extending well beyond the marginal phloem caps. There is a similar development of sclerenchyma in some genera of Ixioideae, and in Iridoideae-Irideae, e.g., *Dietes* (Rudall, 1983), and the shrubby genera of Nivenioideae (Rudall & Burns, 1989). In the last-mentioned two groups the sclerenchyma is not associated with the marginal bundles. There is little doubt that the presence of subepidermal sclerenchyma on the leaf margins is a specialized condition and a synapomorphy for *Watsonia* in addition to those recognized by Goldblatt (1989).

#### DISCUSSION

The five genera of Watsonieae comprise a monophyletic line united by the derived deeply divided style branches and the absence of flavone O-glycosides (Goldblatt, 1989, 1990a). The sister tribe, Ixieae, differs by having a putatively more specialized type of corm ontogeny and by having flavones and flavone O-glycosides. Within Watsonieae, *Watsonia* constitutes one clade and the four remaining genera a second. Several synapomorphies unite the species of *Watsonia* (Goldblatt, 1989), and now the presence of subepidermal mar-

ginal sclerenchyma can be added. The clade formed by *Thereianthus*, *Micranthus*, *Lapeirousia*, and *Savannosiphon* share three synapomorphies: small corms; corm tunics formed only from the cataphylls (the foliage leaves are inserted on the flowering stem and do not contribute to the tunics); and corm tunics composed of densely compacted fibers (previously defined as hard or woody by Goldblatt, 1989). Only subg. *Lapeirousia* has truly woody tunics of a uniform texture and smooth surface. *Thereianthus* and *Micranthus* comprise one clade, defined by their fusiform seeds (Goldblatt, 1989). The presence of complete sclerenchymatous bundle sheaths in the leaves is a possible additional synapomorphy (only three of the ten species in the two genera have been examined for this character), although this xeromorphic feature is a fairly common condition in Iridaceae.

*Savannosiphon*, which is monotypic, and *Lapeirousia* are weakly related (Goldblatt, 1989). They both have angular to winged stems and coriaceous capsules (polarization of the latter character is uncertain). Leaf anatomy makes no contribution to our perception of this clade.

The unusual flat-based corms of *Lapeirousia*, the major synapomorphy for the genus (Goldblatt, 1989), separate it from *Savannosiphon* whose included styles and stamens readily distinguish it from other Watsonieae. The position of the vascular bundles in *Savannosiphon* resembles that in *Pillansia*, but whether this represents a reversal to the primitive state or an indication that the genus is misplaced in our phylogeny (Fig. 3) is uncertain.

Within *Lapeirousia* there appear to be two major groups (Fig. 3) defined by their corm tunics, leaf morphology, and anatomy. Species with woody tunics of uniform texture and a smooth surface, corrugate leaves with truncate ribs, and mostly alternate veins form one clade, which we recognize as subg. *Lapeirousia*. The remaining species are plesiomorphic for these characters (Table 1) but have a presumably derived inflorescence structure (Goldblatt, 1990b), and we recognize the group as subg. *Paniculata*. In general, species of subg. *Paniculata* have highly branched inflorescences (pseudopanicles) (Fig. 4A, B), whereas those of subg. *Lapeirousia* generally have spikes (Fig. 4C), although these may also be branched to some degree. Some members of subg. *Paniculata*, notably *L. abyssinica*, have few-branched inflorescences that are indistinguishable from those of subg. *Lapeirousia*. A simple or few-branched spike is presumed to be the basic condition in Watsonieae and Ixieae (Goldblatt, 1990a, b). Species of subg. *Lapeirousia* have herbaceous bracts that are often

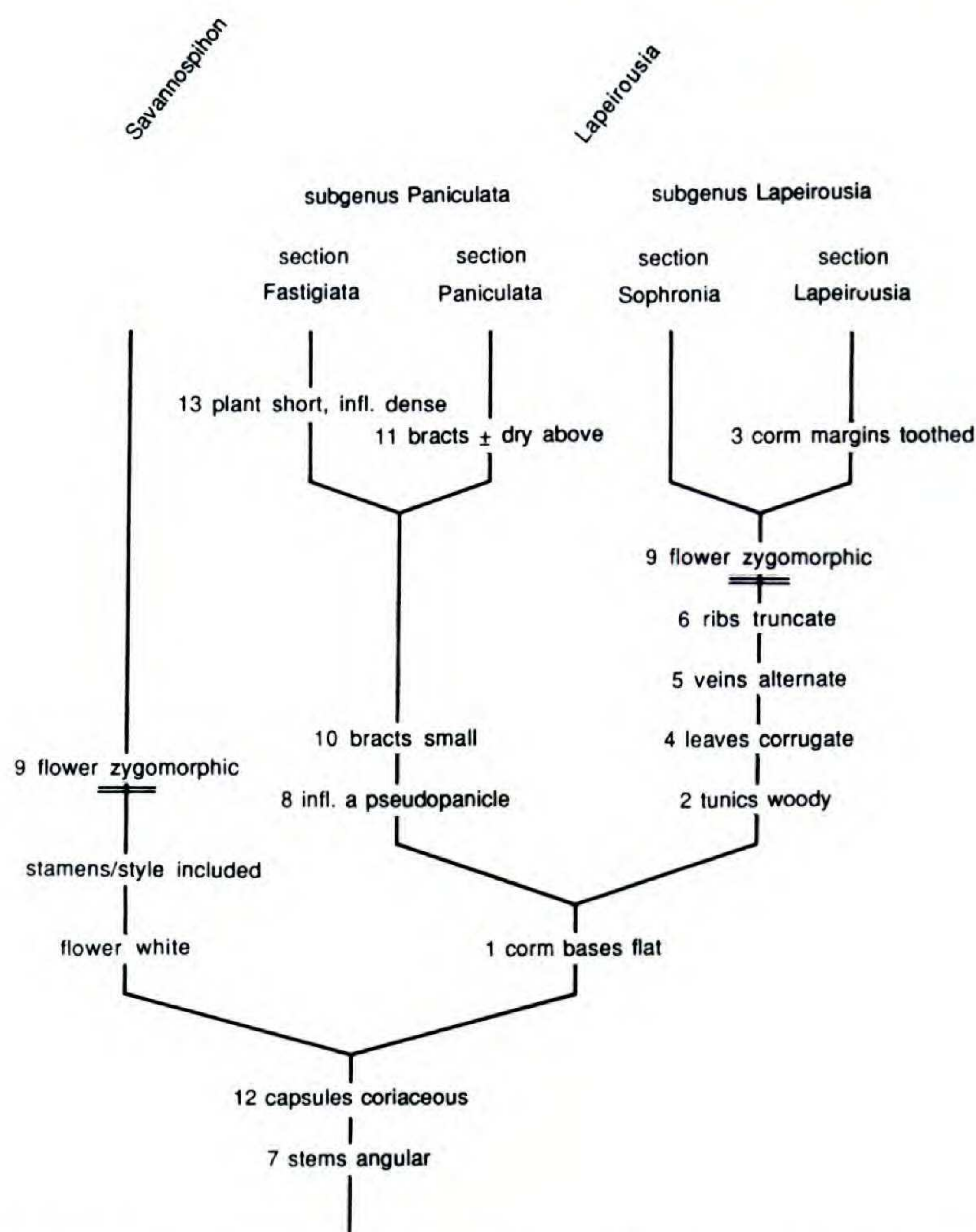


FIGURE 3. Hypothetical phylogeny of *Lapeirousia* showing the major infrageneric lineages and the apomorphic characters that define them. Characters used in the cladogram are listed in Table 3.

enlarged and sometimes ridged, keeled, or toothed. In subg. *Paniculata* the bracts are generally small and either entirely herbaceous or partly membranous and are often dry at anthesis. We assume that small bracts constitute a second, weak, synapomorphy for the subgenus (Table 2), as large, firm herbaceous bracts are the presumed basic condition for the tribe. Thus subg. *Lapeirousia* has diverged in the nature of its vegetative organs whereas subg. *Paniculata* has to some extent in the floral axis.

The occurrence of actinomorphic flowers in three species of subg. *Paniculata*, *L. corymbosa* (from the southwest Cape) and *L. coerulea* and *L. avas-montana* (from Namibia) remains puzzling. These species do not appear to be closely related but they may well be primitive in the subgenus, and there seems no reason to believe that the actinomorphic flower is a derived trait in a genus of largely zygomorphic-flowered species. We accept here that actinomorphy is the primitive condition for the genus and that zygomorphy must have evolved independently in each subgenus of *Lapeirousia* as well as in *Savannosiphon*. There is considerable floral convergence in Ixiodeae, and there are single instances of presumably primitive actinomorphy in

the otherwise zygomorphic-flowered genera *Watsonia* (Goldblatt, 1989) and *Thereianthus* (Lewis, 1941).

By contrast, in subg. *Lapeirousia* the zygomorphy is thought to be the basic state and actinomorphy derived in the few species in which it occurs (Goldblatt, 1972). These actinomorphic species are all acaulescent, and we assume that actinomorphy is adaptive for these low-growing plants whose flowers are borne close to the ground—vertical presentation with consequent actinomorphy enhances floral display and access to long-tongued pollinators.

A further refinement of the infrageneric classification of *Lapeirousia* is suggested by discontinuous patterns of variation in both subgenera (Fig. 3). All the Cape species of subg. *Paniculata* have dark corm tunics, a trait only occasionally found in the tropical African species; fairly short, falcate leaves; rather congested inflorescences; and usually low stature (Fig. 4D). These species also have a basic chromosome number of  $x = 10$  (Goldblatt, 1971, 1972), whereas the tropical species range from  $n = 8$  to  $n = 3$  (Goldblatt, 1990c). The bracts of the tropical species are characteristically dry at anthesis (there are a few exceptions), which we



FIGURE 4. Representative species of *Lapeirousia* showing the morphology of the inflorescence.—A. *L. bainesii* (sect. *Paniculata*).—B. *L. corymbosa* subsp. *fimbriata* (sect. *Fastigiata*).—C. *L. dolomitica* subsp. *lewisiana* (sect. *Lapeirousia*).—D. *L. odoratissima* (sect. *Sophronia*). Scale:  $\times 0.5$ .



assume is a derived state (Table 2). We suggest that the tropical and Cape members of subg. *Lapeirousia* constitute two monophyletic lines for which we propose sectional rank: sect. *Fastigiata* for the Cape species and sect. *Paniculata* for the tropical species.

In subg. *Lapeirousia* those species with the specialization of elaborate, toothed to spiny lower corm tunic margins probably constitute a monophyletic line and also merit sectional segregation. Whether the remaining species constitute one or more lines remains to be determined. We find no reason to favor a particular hypothesis here but suggest they be segregated in one section, which incidentally contains, among others, all the acaulescent species (Baker's subg. *Sophronia*).

#### SYSTEMATICS

**Lapeirousia** Pourret, Mem. Acad. Sci. Toulouse 3: 79–82. 1788. TYPE: *Lapeirousia compressa* Pourret (= *L. fabricii* (de la Roche) Ker).

##### 1. Subgenus **Lapeirousia**

Plants with hard, woody corm tunics of uniform texture, the surface smooth and often glossy, decaying irregularly into unequal fragments, rarely becoming fibrous, the basal margins sometimes produced into teeth or spines. *Stem* aerial or entirely subterranean. *Leaves* corrugate (shallowly plicate), without a prominent midrib and all major veins  $\pm$  equal. *Inflorescence* a simple or branched spike, or the internodes very short and forming a tuft at ground level; *bracts* herbaceous, short to long, the margins and keel sometimes undulate, crisped or toothed, the inner shorter than the outer. *Flowers* actinomorphic (only in acaulescent species) or zygomorphic, short- to long-tubed, the upper tepal usually larger than the others, and the lower three with contrasting markings; stamens symmetrically disposed or unilateral and arcuate.

##### Section **Lapeirousia**

Plants with woody corm tunics with the basal margins toothed or spiny. *Stem* aerial and usually branched. *Inflorescence* a simple or branched spike. *Flowers* always zygomorphic with the stamens unilateral and arcuate.

Eight species occurring in the southwest Cape, Namaqualand and the Karoo, South Africa, and in southern Namibia.

##### Section **Sophronia** (Lichst. ex Roemer & Schultes)

Goldbl. & Manning, stat. nov. *Lapeirousia* subg. *Sophronia* (Lichst. ex Roemer & Schultes) Baker, Handbk. Irideae 174. 1892. *Sophronia* Lichst. ex Roemer & Schultes, Syst. 1: 482. 1817. TYPE: *Lapeirousia plicata* (Jacq.) Diels.

Plants with woody corm tunics with the bases entire, not produced into teeth or spines. *Stem* aerial and usually branched or not produced above the ground. *Inflorescence* a simple or branched spike, or the internodes very short and forming a tuft at ground level. *Flowers* actinomorphic in the acaulescent species or zygomorphic with the stamens unilateral and arcuate.

Ten species mostly in southern Africa, although *L. odoratissima* widespread across south tropical Africa and Namibia.

2. Subgenus **Paniculata** Goldbl. & Manning, subgenus nov. TYPE: *Lapeirousia erythrantha* (Klatt) Baker.

Plantae cormi tunicis duris, fibrosis compactis compositis, foliis usitate planis costatis, raro teretibus, inflorescentia usitate perramoso et  $\pm$  paniculato, bracteis brevibus subaequalibus aliquando siccis supra.

Plants with hard, persistent corm tunics composed of densely compacted fibers (sometimes  $\pm$  woody in texture), decaying into vertical strips or becoming fibrous and cancellate to reticulate. *Leaves* usually plane with the midrib and sometimes other veins raised, or sometimes terete. *Inflorescence* usually highly ramified and  $\pm$  panicle-like (a pseudopanicule) or sometimes a branched spike, the ultimate branches bearing 1–8 flowers, and those below the terminal flower always sessile; *bracts* short, herbaceous, sometimes dry apically or for their entire length at anthesis, the inner bracts about as long as the outer ones.

Seventeen species occurring in the southwest Cape, South Africa, and in tropical Africa from central Namibia to Ethiopia and Nigeria.

Section **Paniculata**. TYPE: as for the subgenus.

Plants usually very branched. *Corm* tunics pale straw to blackish, decaying into regular vertical strips or becoming fibrous and reticulate. *Leaves* plane or rarely terete, the midvein sometimes raised, usually straight, sometimes weakly falcate. *Inflorescence* a pseudopanicule or rarely a branched spike, usually lax but the flowers sometimes congested at the end of the branches; *bracts* herbaceous to membranous, usually becoming dry in the

upper half by anthesis. *Flowers* actinomorphic or zygomorphic, the tepals subequal or unequal (then with the upper tepal largest and reflexed or arched over the stamens); stamens symmetrically disposed or unilateral and arcuate.

Fourteen species extending from central Namibia, Botswana, and the Transvaal across central Africa to Ethiopia in the north and Nigeria in the west.

Section **Fastigiata** Goldbl., Contrib. Bolus Herb. 4: 15. 1972. TYPE: *Lapeirousia corymbosa* (L.) Ker.

Plants usually very branched. *Corm* tunics dark brown to black, decaying into regular vertical strips. *Leaves* plane, the midvein sometimes raised, falcate or straight. *Inflorescence* a pseudopanicule or a spike, usually congested; *bracts* herbaceous, the apices often reddish or purple. *Flowers* actinomorphic or zygomorphic, the tepals subequal; stamens symmetrically disposed or unilateral and arcuate or declinate.

Three species restricted to the southwest Cape, South Africa.

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